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Ecology

Aluminum toxicity and forest decline

(root elongation/Ca uptake/x-ray microanalysis)

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ABSTRACT **The rate of root elongation in seedlings of *Picea abies* was drastically inhibited by exposure to $AlCl_3$ at 800 or 1200 μmol/dm^3 in nutrient solutions. A 35-day exposure to Al at 700 μmol/dm^3 reduced Mg and Ca in roots and needles of the seedlings. The Mg content of needles was reduced to levels considered to be critical for Mg deficiency. In investigations of ^{45}Ca uptake into roots, exposure to Al at 100–800 μmol/dm^3 reduced ^{45}Ca uptake by 77–92%, respectively. By using x-ray microanalysis, the distribution of Al, Mg, Ca, and K was found to be similar in roots of *Picea abies* seedlings grown in solution culture and in roots collected from declining spruce stands at Solling, F.R.G. In solution culture Al displaced Mg and Ca in the root cortex. A mechanism of Al toxicity for root growth and ion uptake is proposed, and its relevance to forest decline is discussed.**

There have been changes in forest health in Europe and North America for several decades (1). In the Federal Republic of Germany "new type" forest decline is attributed to anthropogenic inputs into forest ecosystems (2), among other inputs to acidity. In North America the role of anthropogenic factors cannot be clearly defined (3). In forest ecosystems in the Federal Republic of Germany, the amount of the introduced acidity far exceeds the rates of acid buffering by weathering of minerals (4, 5). The resulting increase in soil acidity induces loss of exchangeable cations (Mg^{2+}, Ca^{2+}, and K^+) and release of normally sparingly soluble aluminum (Al) and heavy metals into the soil solution. The hypothesis that Al toxicity may be a primary factor in forest decline was suggested by Ulrich *et al.* (6). High concentrations of Al have long been known to impair growth of crop plants (ref. 7 and for reviews, see refs. 8 and 9). Disturbances to root systems have been observed in every declining forest stand in the Federal Republic of Germany where root systems have been studied (10). Symptoms of root disturbance include strong vertical gradients of fine root biomass (11), increased percentage of dead fine roots in damaged stands compared to undamaged stands (11), and changes in chemical composition (11, 12). Ingrowth core studies showed that changes in root systems are due to soil conditions and not to deficiency of assimilates.

In solution culture, root growth was inhibited by levels of Al similar to those found in forest soils (13). The concentration of Al in itself was not critical, but the molar ratio of Ca/Al was critical. Ca reduced the toxic effects of Al. Exposure to Al also disturbed the mineral nutrition of tree seedlings. Reduced Ca and Mg were found in *Picea abies* (14), *Picea rubra* (15), and *Abies balsamea* (15) exposed to Al. An ameliorating effect of Mg and Ca on the effects of Al could again be found (14).

In Norway spruce, symptoms of decline are premature loss of the older needles and discoloration of the remaining needles. In older needles the discoloration ranges from a yellowing of the tips to complete yellowing of the whole needle. In current-year needles, a red-brown discoloration is found; this, however, is less common than that of the older needles. Discoloration can often be associated with nutritional imbalances, in particular with lack of Mg and Ca in the needles (16).

In the present work, the influence of Al on root elongation, on the mineral content of roots and needles, and on the distribution of minerals in roots of spruce is investigated, and a mechanism of Al toxicity is proposed. The role of Al in forest decline is discussed.

MATERIALS AND METHODS

Culture of Plant Material. *Tree seedlings.* Seeds of *Picea abies* (L.) Karst were surface-sterilized in 1% $Ca(OCl)_2$ in 10% (vol/vol) ethanol and germinated on 1% water agar. Seedlings were then transferred to an aseptic nutrient solution [(in μmol/dm^3) 130 Ca, 82 Mg, 350 K, 644 NO_3, 16 PO_4, 85 SO_4, 174 Na, 5 Fe, 67 Cl, 3 Mn, 5 B, 0.1 Mo, 0.1 Cu, and 0.1 Zn (pH 3.8)] and grown for 7 days.

Nutrient solutions were constantly aerated with sterile air. All work was carried out at 23/21°C day/night temperatures, at a light intensity of 100 μmol·m^{-2}·s^{-1} (Osram L 18 W/25 lamps) with a 16-hr photoperiod. Seedlings were transferred to nonsterile nutrient solutions and grown for 9 days in solutions containing Al at 800 or 1200 μmol/dm^3 as $AlCl_3$ (Ca/Al molar ratio = 0.16 and 0.1, respectively) or for 35 days in Al at 700 μmol/dm^3. Controls were grown in the absence of Al throughout. All solutions were adjusted to pH 3.8, and the nutrient solutions were renewed daily.

Two-year-old saplings. Seed of *Picea abies* was germinated, grown in commercially available soil, and maintained for 2 years under greenhouse conditions. Roots were carefully washed free of soil and transferred to aerated nutrient solutions (13). The saplings were grown for 123 days in the presence or absence of Al at 2000 μmol/dm^3 (Ca/Al molar ratio = 0.05) at pH 3.8 at 20/22°C day/night temperatures, a light intensity of 100 μmol·m^{-2}·s^{-1} (Philips TLM 115 W/33 RS lamps), and photo periods of 16 hr for the first 104 days and of 13 hr for the remaining 19 days. Nutrient solutions were changed once weekly.

Root Elongation. Rates of root elongation were determined as described (17).

^{45}Ca Uptake. Five-week-old seedlings were transferred to nonsterile nutrient solutions, allowed to equilibrate overnight, and then transferred to nutrient solutions containing ^{45}Ca at 1.8 MBq/dm^3 for 30 hr. Uptake of ^{45}Ca and the total Ca content of the roots were estimated after 10, 20, 30, 45, and 60 min and after 2, 4, 8, 23, and 30 hr.

To estimate the influence of Al on ^{45}Ca uptake, seedlings were transferred to nutrient solutions containing ^{45}Ca and various concentrations of $AlCl_3$ (0–800 μmol/dm^3) for 1 hr. After the uptake periods, the roots were blotted, excised from the shoots, and dried to a constant weight. Samples

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were wet-ashed in $HClO_4$ at 180°C and taken to dryness, and the ash was dissolved in 1% (wt/vol) HCl. ^{45}Ca activity was determined by liquid scintillation (Philips LSA5). Total Ca was estimated by atomic absorption spectrophotometry.

Collections of Field Samples. Root samples were collected from 100-year-old declining spruce stands at Solling, F.R.G., by using a soil core borer. Roots in the mineral soil (0–5 cm) were carefully freed from the soil, cut into 2-mm segments, and immediately prepared for x-ray microanalysis (see below).

Mineral Analysis. Root and needle material was dried to a constant weight and wet-ashed in $HNO_3/HClO_4$, 3:1 (vol/vol). K, Ca, Mg, and Al were determined by atomic absorption spectrophotometry (Perkin–Elmer, AAS 3030).

X-Ray Microanalysis. Roots from laboratory studies and those collected at Solling were shock-frozen (in isopentane cooled with liquid nitrogen), freeze-dried, and embedded in plastic. The infiltration of the plastic mixture was carried out by using vacuum and pressure as described by Fritz (18). A detailed description of the method will be published elsewhere. Water-free conditions during the entire embedding procedure prevent displacement of water-soluble materials. Measurements of x-ray spectra at various locations throughout a vacuole reveal similar element contents, which normally differ markedly from the element contents of cytoplasm and cell wall of the same cell. This is taken as an indication that major displacements of ions during the preparation do not occur.

Sections 1 μm thick were cut with dry glass knives and an ultramicrotome, transferred to folding grids, coated with a carbon layer, and stored over silica gel.

X-ray microanalysis was carried out by using a Philips model EM 420 electron microscope equipped with an energy dispersive system, EDAX 9100. The accelerating voltage was 120 keV (1 eV = 1.602×10^{-19} J), and the diameter of the analyzed area was 200 nm. The content of the elements at the analyzed spots is represented as the net count rate of the peaks (in cps) above the background. As all measuring parameters (e.g., beam current or tilt angle) were kept constant, this is suitable for comparison of element contents within one section and between different sections but does not permit a statement about the absolute concentration of the elements. The root samples prepared for microanalysis were selected for comparable xylem differentiation such that the primary xylem was fully developed.

RESULTS

Root Elongation. The rate of root elongation of seedlings exposed to Al at 800 or 1200 μmol/dm^3 was inhibited by 63–73% compared to the control within 24 hr of exposure (Fig. 1). The rate of root elongation decreased further on day 2, after which a constant rate of growth of ≈0.2 mm/day was maintained for the remainder of the treatment period.

^{45}Ca Uptake. The uptake of ^{45}Ca could be divided into two phases, an initial rapid phase over the first 60 min followed by a linear uptake (Fig. 2). Over the 30-hr uptake period the total Ca content of the roots was unaltered, indicating that there was no appreciable net uptake of Ca. The ^{45}Ca uptake represents an exchange of ^{45}Ca for Ca within the root.

The uptake of ^{45}Ca was severely reduced by the presence of Al (Fig. 3). In the presence of Al at 100 μmol/dm^3 (Ca/Al molar ratio = 1.3) uptake of ^{45}Ca was reduced by 77% after the 1-hr treatment. At higher Al levels the uptake of ^{45}Ca was further reduced.

Mineral Nutrition. In seedlings exposed to Al at 700 μmol/dm^3 for 35 days, the mineral contents of roots and needles were determined (Table 1). In seedlings exposed to Al, an 8 times greater concentration of Al was found in the roots compared to the needles. The Ca and Mg in roots and needles decreased after exposure to Al. After Al treatment, a proportionally greater decrease in Mg content was found in roots than in needles, whereas for Ca a greater decrease was found in the needles than in the roots. K content was not affected by exposure to Al in either roots or needles.

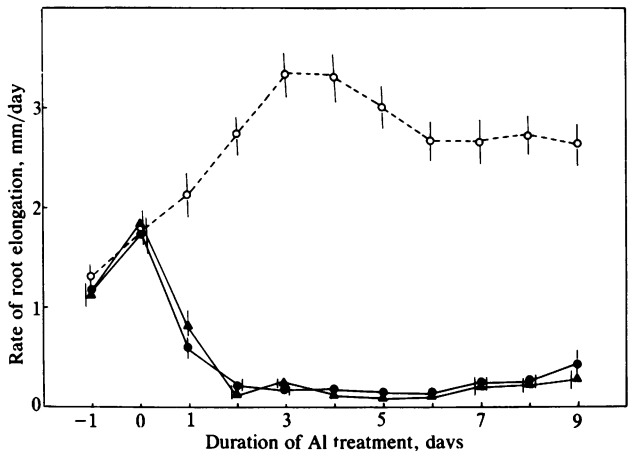

FIG. 1. Root elongation rate of 4-week-old *Picea abies* seedlings grown for 9 days in nutrient solutions containing Al at 0 (○), 800 (●), or 1200 (▲) μmol/dm^3 as $AlCl_3$ is shown. Bars indicate the standard error. Each point represents the mean of 30 replicates.

X-Ray Microanalysis for Saplings Grown in Solution Culture. *Al.* In Al-treated roots the Al content of cell walls of the cortex was high (Fig. 4). Al values comparable to those measured in the cortex were also found in the outer walls of the endodermis cells. A very drastic reduction in Al content occurred in the radial walls of the endodermis. In the inner walls of the endodermis cells the Al content was very low. Even lower amounts of Al were found in the outer cell layers of the central cylinder. In walls of parenchymal cells of the inner part of the central cylinder and in secondary walls of the tracheids, Al could not be detected (Fig. 4).

In control roots (Fig. 5), some Al was also detected in the walls of the cortex cells. In inner walls of the endodermis and cell walls of the central cylinder, Al could be detected only at a few points.

Ca. In the cortex cell walls of Al-treated roots, Ca could only be found in low amounts (Fig. 4). Low Ca values were also measured in the inner walls of the endodermis cells. In walls of the outer cell layers of the central cylinder the Ca content was high. Even higher Ca contents were found in walls of nontracheidal cells of the inner central cylinder,

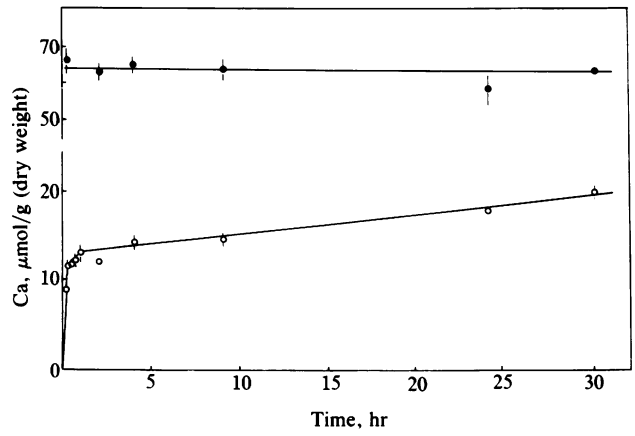

FIG. 2. ^{45}Ca (○) and total Ca (●) are shown [as μmol/g (dry weight)] in roots of 4-week-old *Picea abies* seedlings exposed to nutrient solutions labeled with ^{45}Ca at 1.8 MBq/dm^3 for 30 hr at 25°C. Bars indicate standard error.

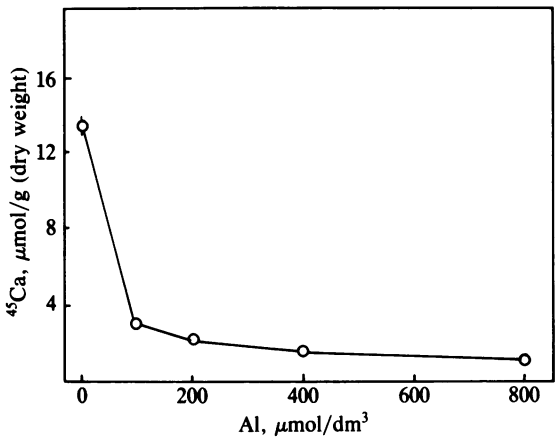

FIG. 3. ^{45}Ca [μmol/g (dry weight)] in roots of 4-week-old *Picea abies* seedlings grown in nutrient solution is shown. Roots of intact seedlings were exposed to nutrient solutions labeled with ^{45}Ca at 1.8 MBq/dm^3 and containing a range of $AlCl_3$ concentrations (0–800 μmol/dm^3) for 1 hr at 25°C. Bars indicate standard error.

reaching at some points >800 cps, which are responsible for the high standard deviation of the Ca content of this region (Fig. 4).

In control roots (Fig. 5), the Ca content of the cortical cell walls was much higher than in the Al-treated roots, whereas the inner walls of endodermis cells had a low Ca content. In the central cylinder the Ca content reached values comparable to those in the cortex cell walls (Fig. 5) but on average was not as high as those in the central cylinder of the Al-treated roots.

Mg. In the whole cortex and endodermis of the Al-treated roots (Fig. 4), the Mg content at nearly all analyzed points of the cell walls was below the limits of detection. In the outer cell layers of the central cylinder Mg was just detectable. In cell walls of the inner central cylinder Mg was not detectable. In the control root cortex (Fig. 5), the Mg content was low, but in all analyzed points of the cell walls it was clearly detectable. In nontracheidal cell walls of the whole central cylinder (Fig. 5), Mg reached rather high values, 45 cps in the outer cell layers and 30 cps in the inner part of the central cylinder. This is >10 times more than in the Al-treated roots.

K. K was chosen as an example of an element that is often found in similar amounts in comparisons of damaged and healthy trees. The K content in cell walls of the whole root was high, except for the inner wall of the endodermis cells. No major differences could be found in Al-treated and control

Table 1. Mineral elements in needles and roots of *Picea abies* seedlings grown in the presence or absence of Al

Mineral element	Tissue	Mineral element content of tissue, μmol/g (dry weight) −Al	+Al
Al	Roots	4.9	95.0*
	Needles	1.4	12.3*
Mg	Roots	48.9	19.5*
	Needles	50.3	30.3*
Ca	Roots	35.6	25.8*
	Needles	34.3	19.8*
K	Roots	445	436
	Needles	323	335

Picea abies seedlings were grown in nutrient solutions in the presence or absence of Al at 700 μmol/dm^3 as $AlCl_3$ for 35 days. Mineral elements in needles and roots were measured.
*Significantly different mineral element content (P = 0.01).

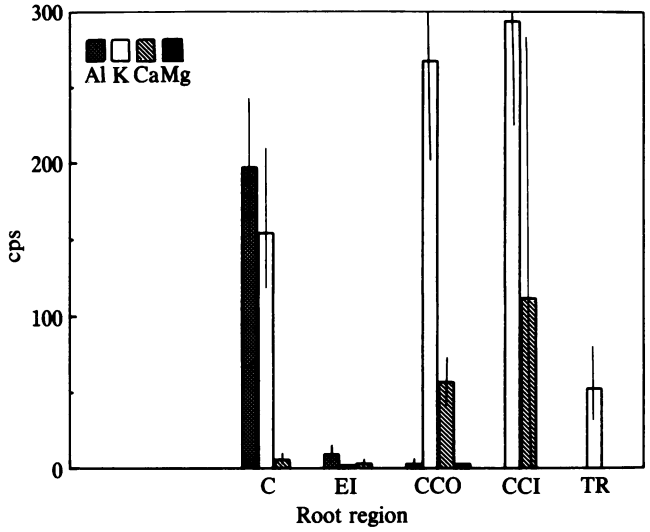

FIG. 4. Al, K, Ca, and Mg in cell walls of roots of *Picea abies* seedlings grown for 123 days in nutrient solutions containing $AlCl_3$ at 2000 μmol/dm^3. Contents expressed in x-ray counts per second (cps). C, cortex; EI, inner tangential walls of endodermis cells; CCO, outer cells of the central cylinder; CCI, inner nontracheidal cells of the central cylinder; TR, secondary walls of tracheids. Bars indicate standard deviation.

roots, but there was a tendency to higher K values in walls of cortex and outer central cylinder cells of Al-treated roots (Figs. 4 and 5).

X-Ray Microanalysis for Roots Collected at Solling. *Al and Fe.* High contents of these potentially toxic elements were found in walls of root cortex cells (Fig. 6). Walls of the mycorrhizal hyphae of the Hartig net contained much less Al and Fe, about one-third of the content of the root cortex cell walls (Fig. 6). Even less Al and Fe were found in the walls of the outer layer of the mycorrhizal hyphae surrounding the roots (Fig. 6).

The Al and Fe contents of inner walls of endodermis cells were very low. In walls of the central cylinder cells Al and Fe could not be detected.

K. K was found in the cortex and stele (except in inner cell walls of the endodermis cells) in rather high amounts (Fig. 6). Much less K was found in the walls of the Hartig net hyphae and of the outer hyphae layer (Fig. 6).

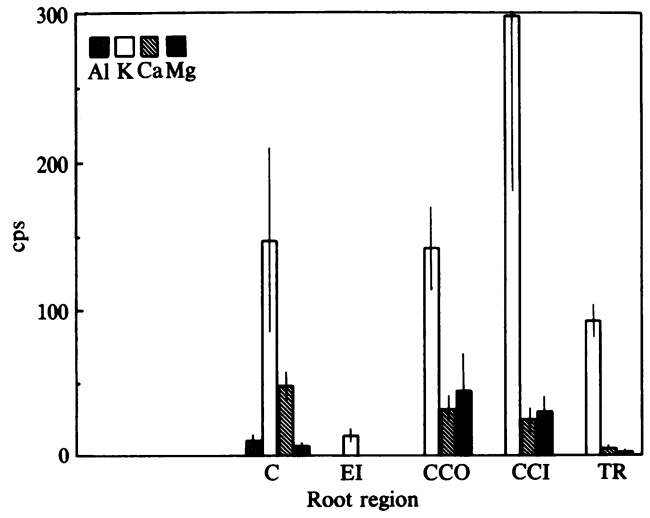

FIG. 5. Al, K, Ca, and Mg in cell walls of roots of *Picea abies* seedlings grown for 123 days in nutrient solutions without Al. Contents expressed in x-ray counts per second (cps). Root regions are as in Fig. 4. Bars indicate standard deviation.

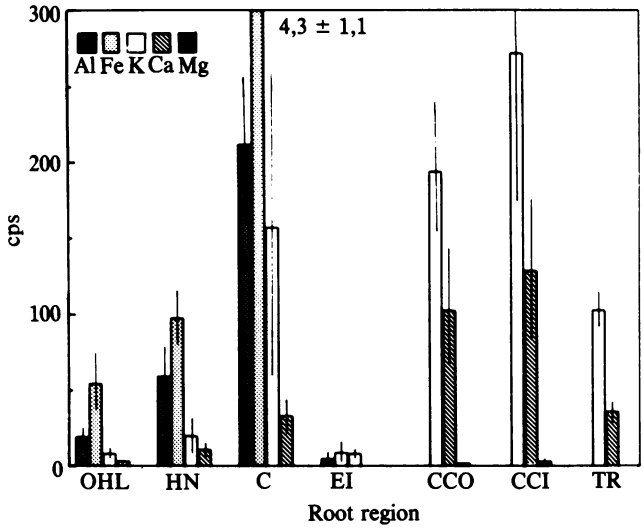

FIG. 6. Al, Fe, K, Ca, and Mg in cell walls of *Picea abies* fine roots taken from the upper mineral soil at Solling, F.R.G. Contents expressed in x-ray counts per second (cps). OHL, outer hyphae layer of the mycorrhiza; HN, Hartig net of the mycorrhiza. Abbreviations for the other root regions are as in Fig. 4. Bars indicate standard deviation.

Ca. The Ca content of the stele was high (Fig. 6). Lower Ca content was found in the cortex (Fig. 6) that was, however, not as low as in Al-treated roots in solution culture. Low Ca amounts could be detected in mycorrhizal hyphae (Fig. 6).

Mg. Mg was detectable only in the stele in low amounts, and at concentration similar to that in roots grown in the presence of Al in solution culture.

DISCUSSION

Al toxicity is considered to be a predisposing factor in forest decline (19) that reduces root growth and inhibits uptake of mineral nutrients. Studies with ^{45}Ca indicate the low levels of Al required in solution to induce ion antagonism. As little Al as 100 μmol/dm^3 reduced ^{45}Ca uptake by spruce roots. In ^{45}Ca exchange studies, Macklon (20) showed that the half-time for exchange of Ca from the Donnan free space is ≈18 min. This is similar to that found for Sr in the Donnan free space of beet disks (21). The half-time for exchange in the cytoplasm was estimated to be 55 min in onion roots (20). As exchange reaches completion in each cell compartment after a period >5 half-times, the rapid ^{45}Ca uptake phase over the first hour represents uptake primarily into the root apoplast. The Al inhibition of ^{45}Ca uptake indicates that Al displaces Ca from the apoplast and thus reduces the number of exchange sites for ^{45}Ca uptake. X-ray microanalysis of Al-treated roots demonstrates that displacement of Ca and Mg occurs in the apoplast of the cortex cells and that the endodermis represents a distinct barrier for Al. The exchange of Al for Ca and Mg in the cell apoplast may be a mode of Al toxicity estimated in terms of root growth. As Ca is an important element for maintaining cell wall structure (22), the exchange of Ca and Mg for Al may inhibit cell elongation. However, other authors have clearly shown that short-term exposure to Al inhibits cell division in root meristems (23, 24). The blocking of cell division may be due to binding of Al to DNA (25). The inhibitory effect of Al on root growth was seen in seedlings exposed to Al at 800 or 1200 μmol/dm^3 (Ca/Al ratio 0.16 and 0.1, respectively). Göransson (26) could also show growth inhibition of *Picea abies* seedlings at Al concentrations >400 μmol/dm^3 by using other culture methods. In long-term measurements of soil solutions under a declining spruce stand at Solling, Ca/Al ratios are between 0.1 and 0.2, and Al concentrations reach 1000 μmol/dm^3 during acidification pushes (27, 28). Although comparison between nutrient solutions and soil solutions must be viewed with some caution, the data indicate that the levels of total Al present in the soil solution are capable of severely reducing root growth. Investigations of Al in soil solutions (29, 30) have shown that Al exists in a number of organic and inorganic complexes and that these must be considered when evaluating the effects of Al on tree growth. However, a similar pattern of distribution was found for the elements Al, Ca, Mg, and K in root sections from both laboratory and field samples. These data support the hypothesis that nutrient solutions used here, the composition of which was based on long-term measurements of soil solutions at Solling, and the soil solution at Solling exposed the plants to a similar ionic environment. The presence of a mycorrhizal sheath did not exclude Al from the cortex cells.

Deficiency of Mg and Ca in needles of declining trees is considered to be a major factor in forest decline (2). In seedlings exposed to Al, the content of Mg and Ca in the needles was significantly reduced. After a 35-day exposure to Al, the Mg contents were similar to those considered to be critical for Mg deficiency in spruce (16). As an intact endodermis appears to be a barrier that limits radial transport of Ca and Mg, the displacement of Mg and Ca in the older regions of the cortex cannot account for the reduced contents of these elements in needles. Mg and Ca used for long-distance transport is predominantly taken up at the root tips (31, 32). For Mg, the stelar tissue of Al-treated roots and roots from Solling were depleted of Mg to just detectable levels. Al may prevent Mg from reaching the stele and, hence, from being transported to the needles. For Ca, however, high amounts were found in the stele in Al-treated and Solling roots as compared to the control. The Ca contents increased toward the root basis (E.F., unpublished data), indicating that Ca transport from root to shoot may be inhibited. In studies where the mineral contents of foliage and root growth have been estimated, Al decreased the concentration of Mg and Ca in birch (33) and spruce seedlings (D.L.G., unpublished data) at concentrations that did not inhibit root growth. It may be speculated that in forest stands with low availability of nutrients, low levels of Al that do not inhibit root growth may be sufficient to critically reduce uptake of Ca and Mg.

Comparison of field and laboratory data is difficult. However, the distribution of elements in roots in our study are very similar, suggesting that the roots were exposed to similar chemical environments. The data show that the high levels of Al found in the soil solution at Solling could account for the root damage and for mineral imbalances found in roots and needles of declining trees. Hüttl† showed that NH_4Cl extracts of soils from declining tree stands in the Black Forest had Ca/Al molar ratios of 0.03–0.04. Needle analysis showed that trees in these stands were also suffering from Mg deficiency. Hence, the mechanism proposed here may also be applicable to other forest areas.

†Hüttl, R. F., 18th International Union of Forest Research Organizations World Congress, Sept. 7–12, 1986, Ljubljana, Yugoslavia, p. 774.

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